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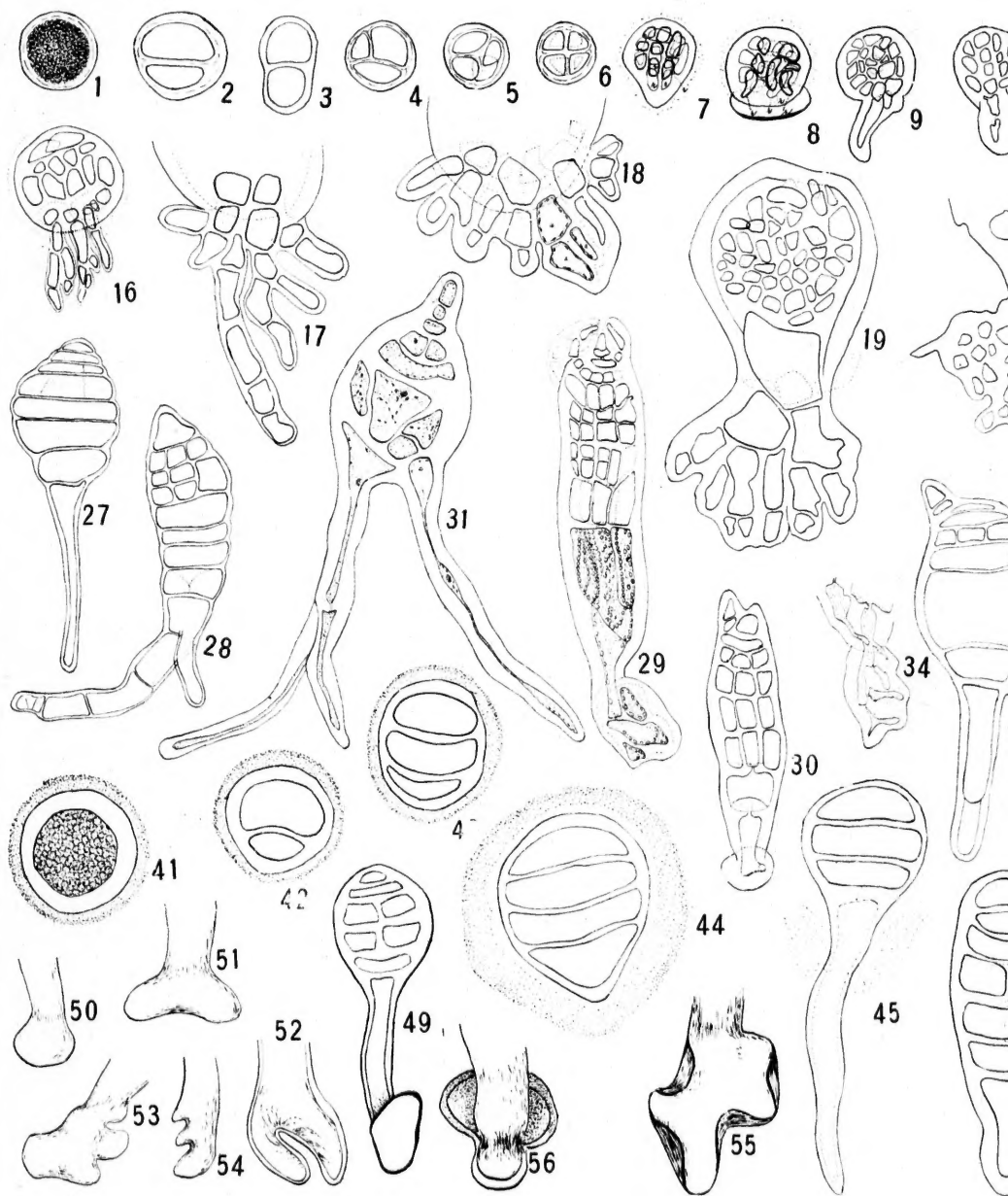
NO. 8—NOTES ON THE DEVELOPMENT OF THE HOLDFASTS
OF CERTAIN FLORIDEÆ.

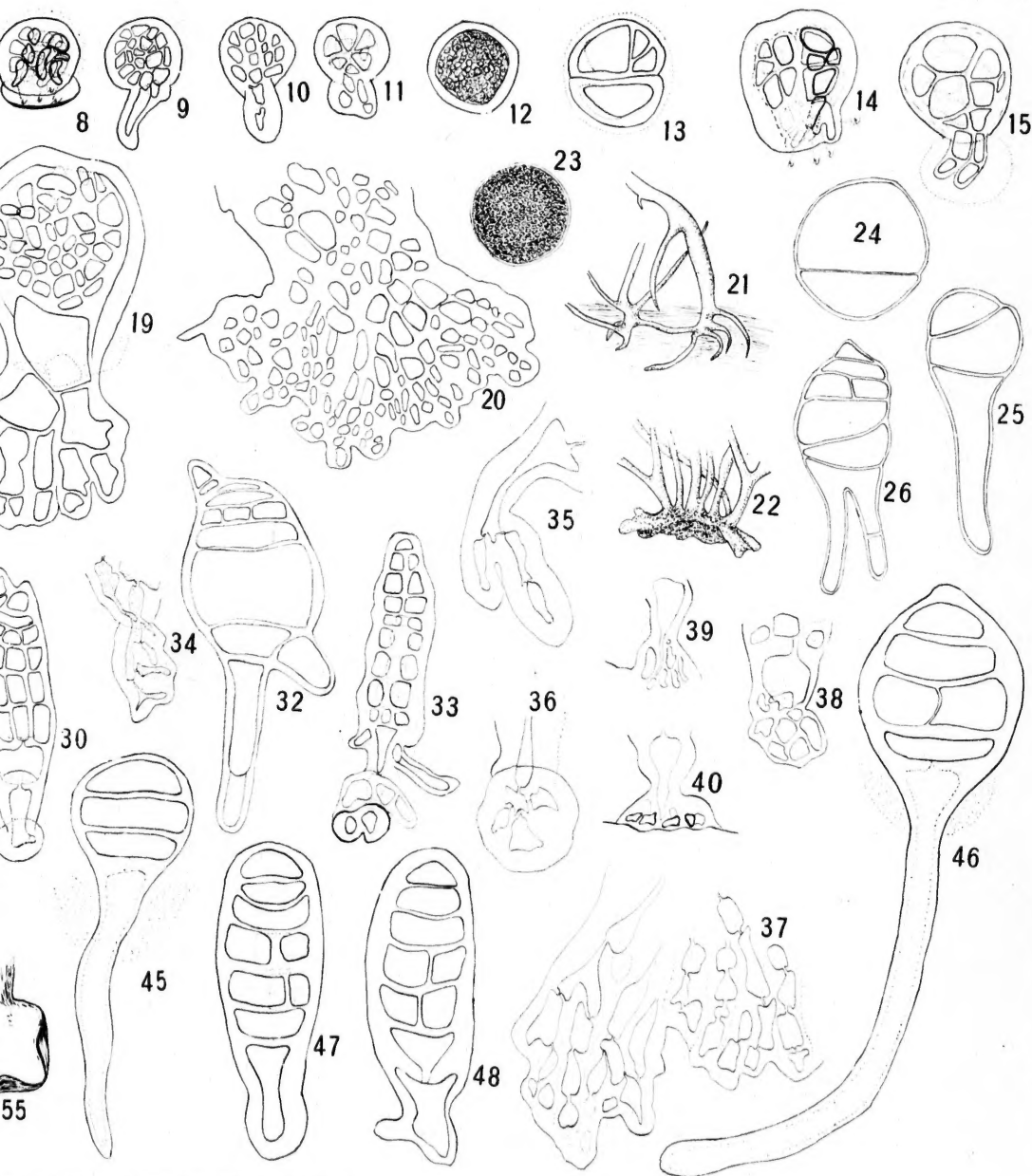
BY
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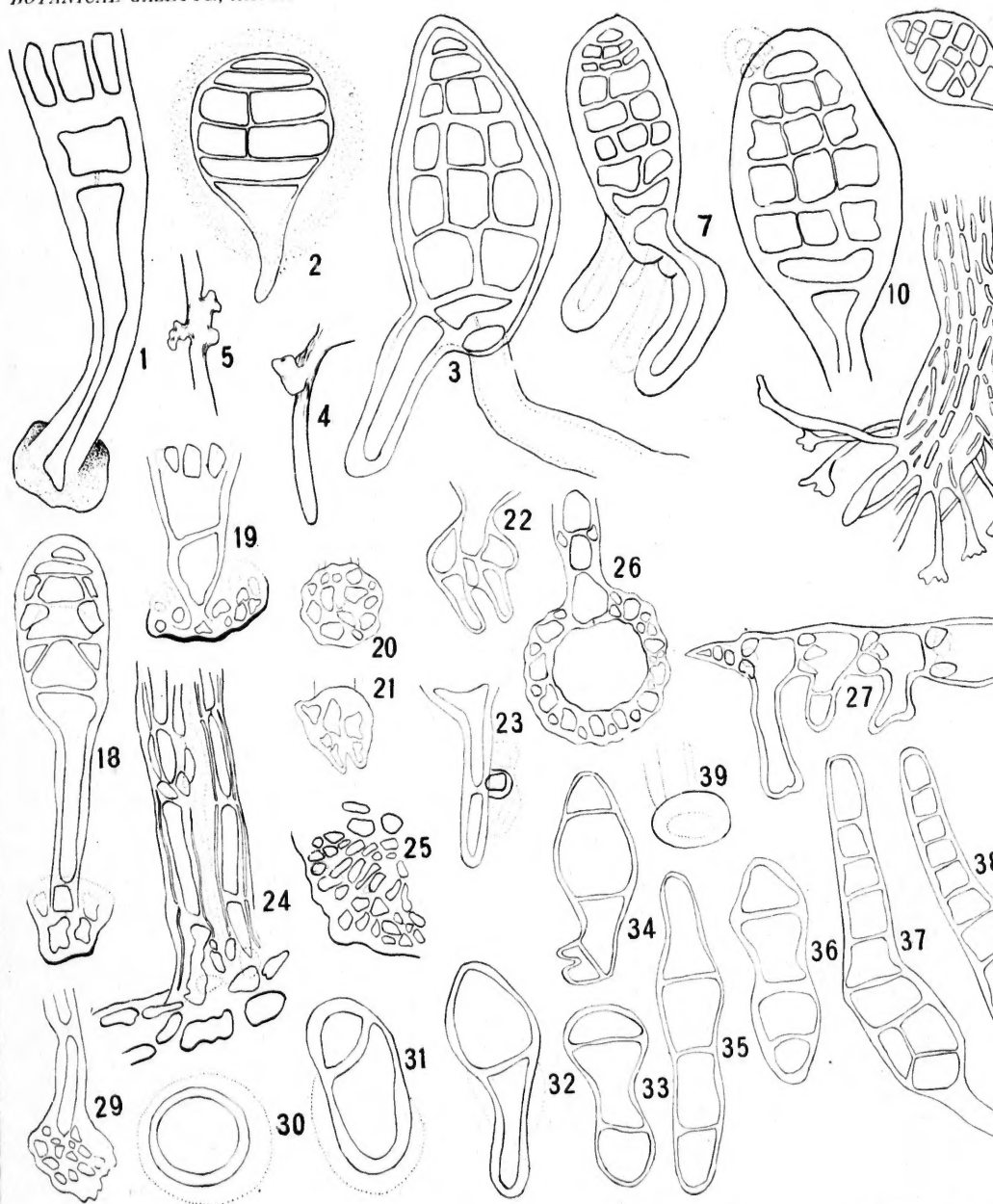
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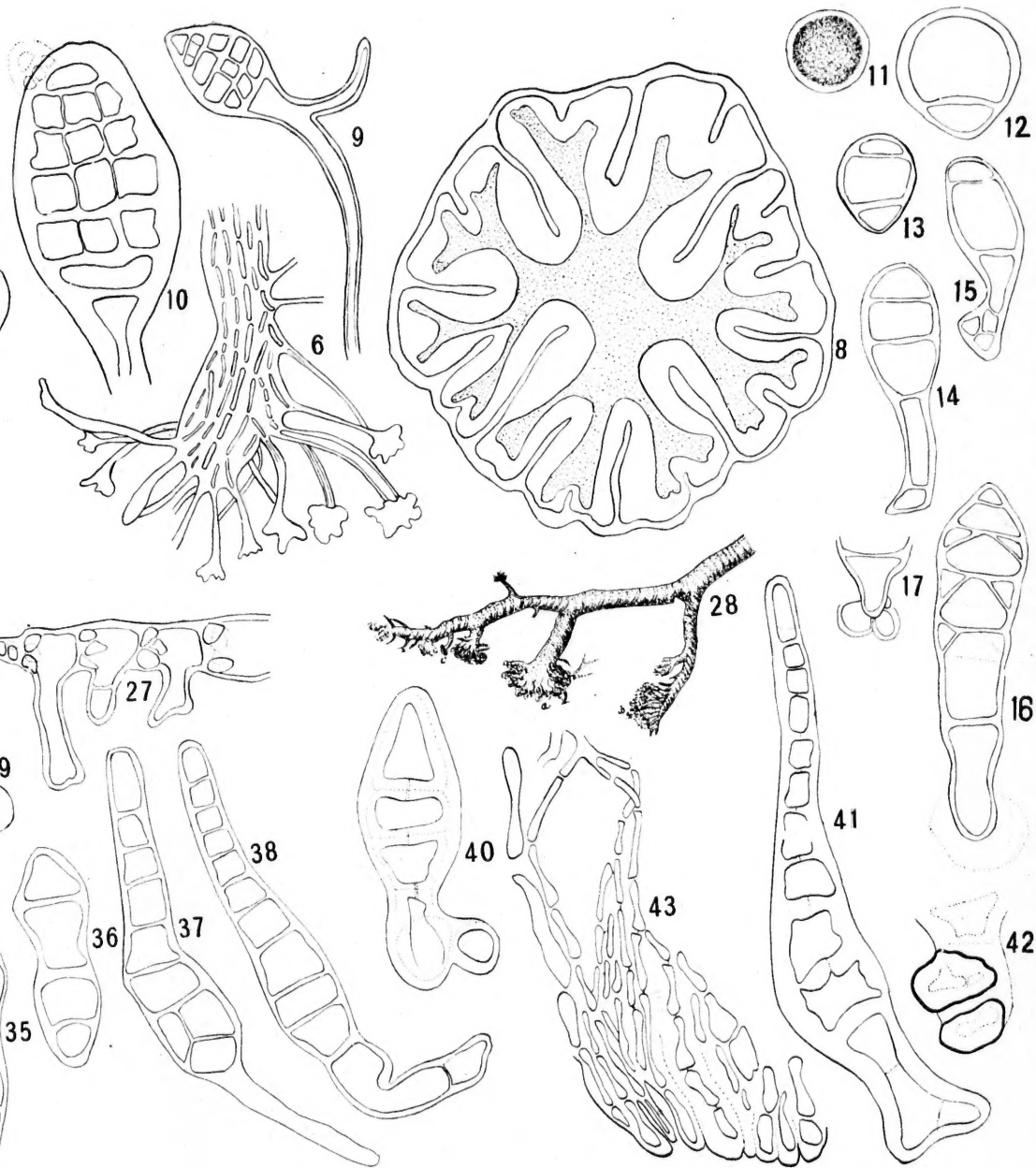
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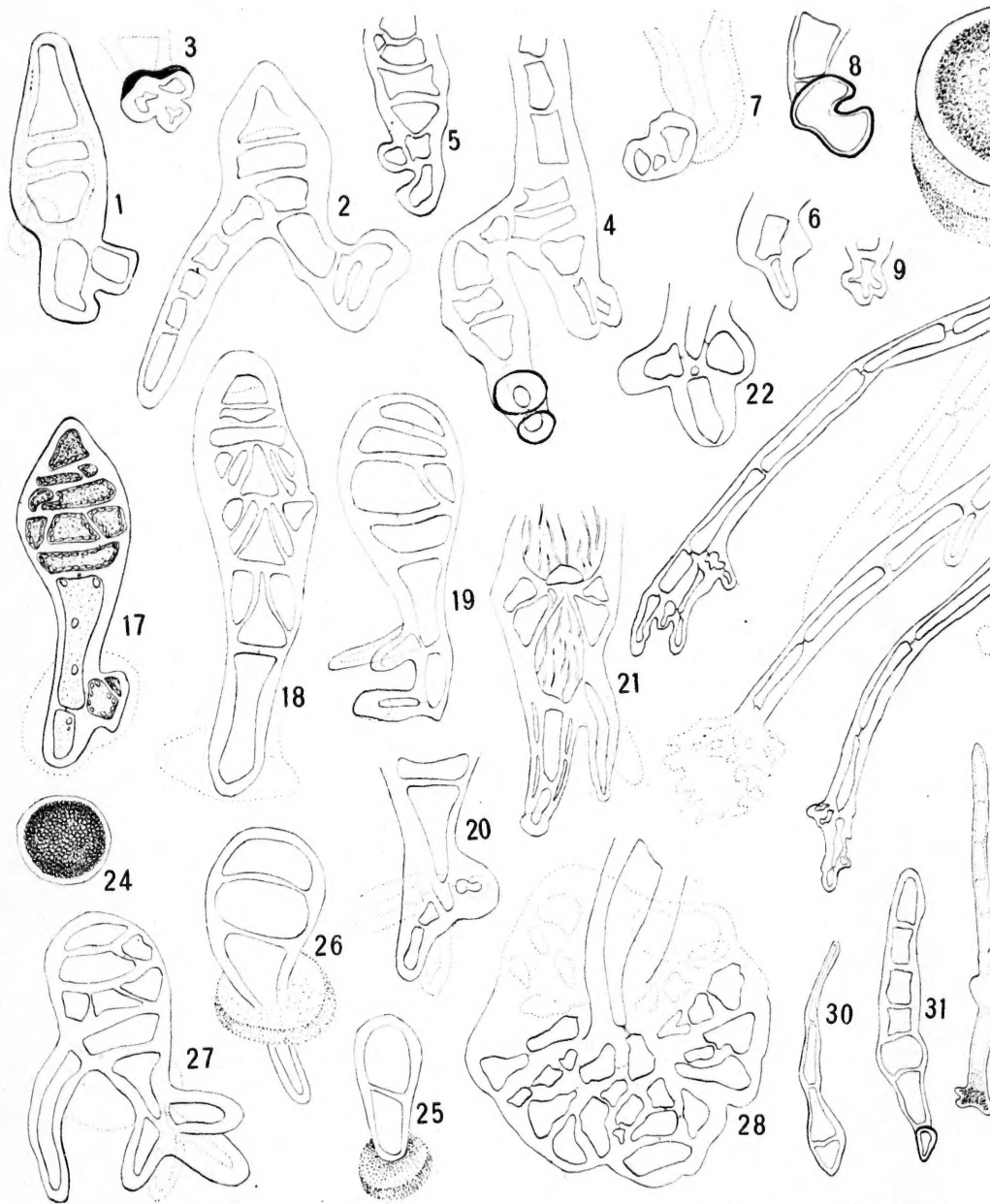
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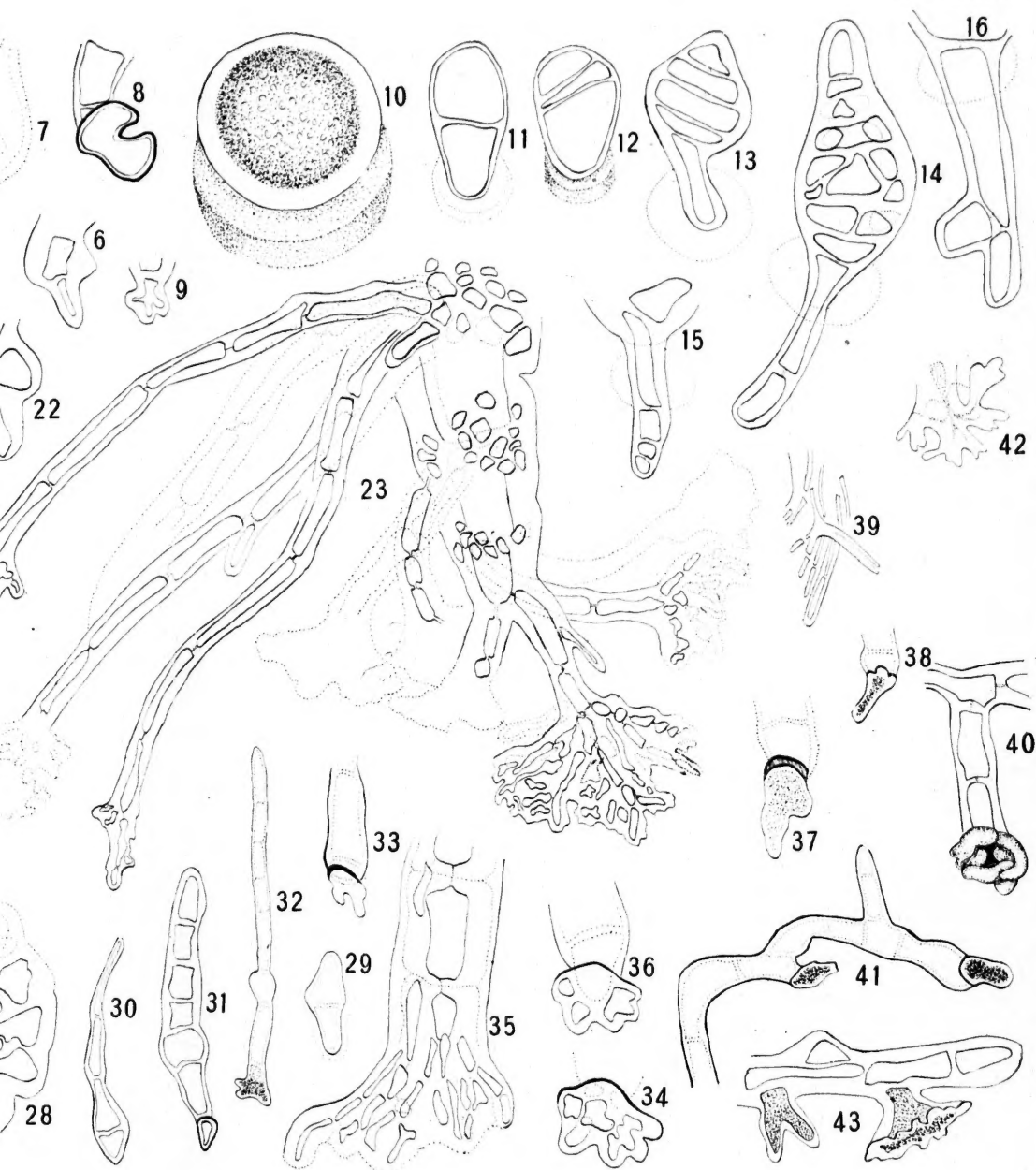


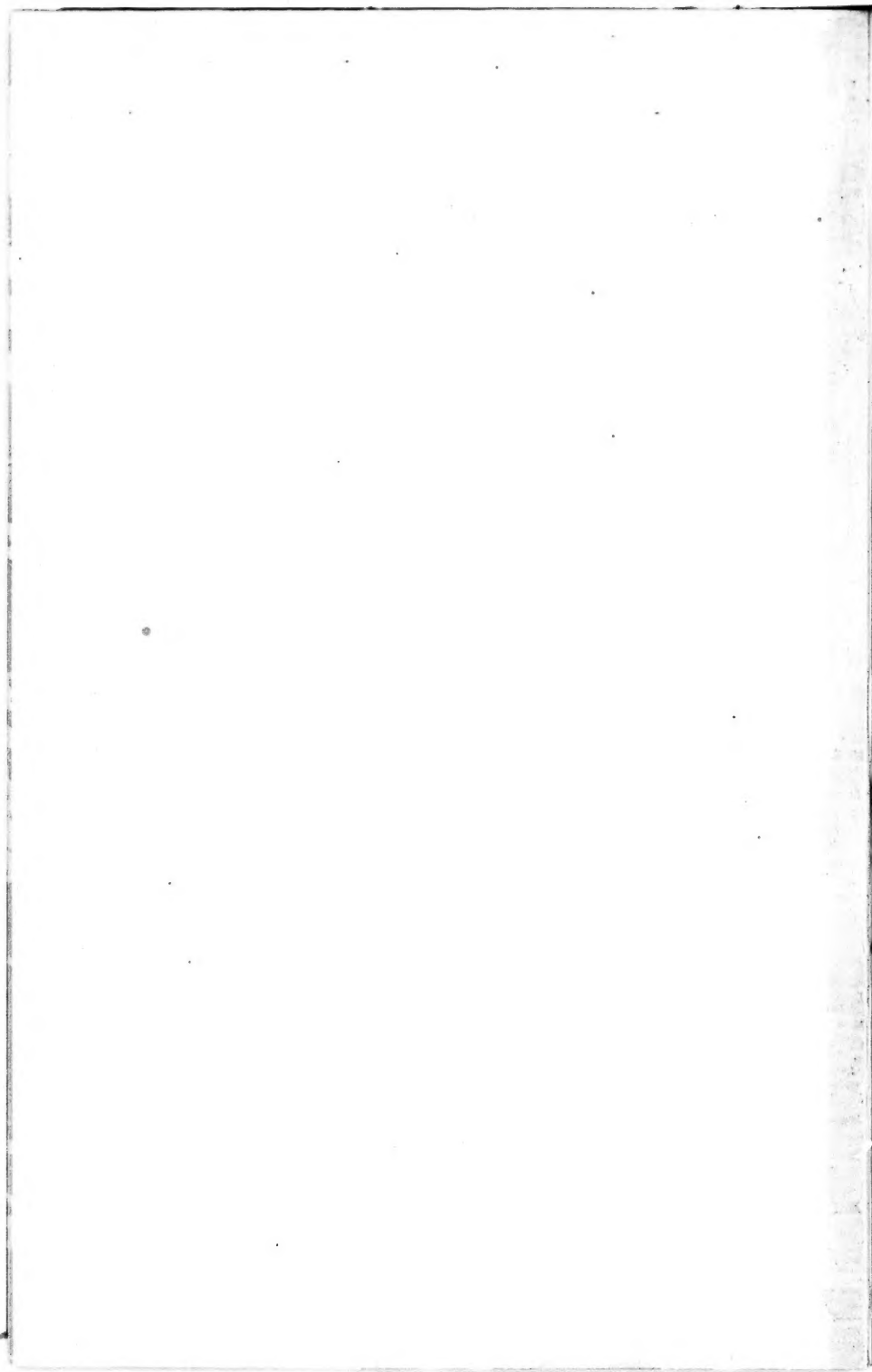














NOTES ON THE DEVELOPMENT OF THE HOLDFASTS OF CERTAIN FLORIDEÆ.

CARRIE M. DERICK.

(WITH PLATES XXI-XXIII AND FIVE TEXT-FIGURES)

WITH the exception of passing references in various works, two articles, the one by Borge (1), the other by Strömfelt (8), include, I believe, all that has been written upon the holdfasts of the algæ. The former deals with a few members of the Chlorophyceæ; the latter is very comprehensive, but it is without illustrations and gives no specific details. Therefore, the study of the development of the holdfasts of some nearly related species of the Rhodophyceæ has seemed advisable.

The observations described in this paper were made at the Marine Biological Laboratory, Woods Hole, Mass., during the summers of 1896 and 1897, and the work was finished in the Botanical Laboratory of McGill College.

Cultures of the spores of several species were made under various conditions. Ordinary glass object-slides were placed in flat porcelain dishes, either white or painted black. The vessels were filled with filtered sea-water and in them were laid plants bearing ripe spores. The spores usually sowed themselves in twenty-four hours, in which case the plants were removed. Some of the dishes were fed by a gentle stream of running water, others were disturbed only three times a day, when the water was drawn off by a siphon and replaced by filtered sea-water. The latter method proved much the better of the two.

The color of the background had no effect upon the development of the spores, nor were the plantlets heliotropic. Cultures kept in a shaded place flourished best, even a short exposure to direct sunlight killing plantlets. It is to be regretted that no record of variations in the temperature and the density of the water was kept. Oltmanns (6) has conclusively shown that such

variations are most important factors in the life and distribution of marine algæ, but a comparison of many cultures of the same species indicates that differences in the conditions which prevailed in the laboratory affected neither the form nor the order of development of the plantlet. It was difficult to keep the young plants healthy for more than three or four weeks; and during a few days of intense heat, in August 1896, all ceased to grow, were attacked by bacteria, and finally died.

Both carpospores and tetraspores were germinated and most closely resembled one another in their development. In some cases, however, tetraspores attached themselves to the substratum less readily than carpospores. This is regarded by Brannon (2) as an adaptation to the immediate distribution of the species.

Every day, slides upon which spores were growing were examined and drawings of living plantlets were made. Permanent mounts for comparative study were prepared at regular intervals and mature holdfasts were preserved in alcohol or in 5 per cent. formalin in sea-water.

The species selected for investigation belonged to the Rhodymeniales, with the exception of one member of the Rhodophyllidaceæ, *Rhabdonia tenera* J. Ag. The carpospores of this alga attach themselves firmly to the slides in nine hours; a very delicate outer layer, probably of mucilage, may be observed, but can hardly be distinguished from the cell-wall (*Pl. XXI, fig. 1*). In a few cases, an irregular layer of a coarsely granular substance surrounded the plantlets, and in one, a thick mucilaginous disk was developed at the base; these appearances were most exceptional, and were doubtless due to slightly abnormal conditions (*Pl. XXI, figs. 7, 8*). After attaching themselves, the spores immediately enter upon a segmentation stage, and within twenty-two hours two divisions are made. The first separates the spore by means of a vertical wall into two equal cells (*Pl. XXI, figs. 2, 3*). Three and four-celled stages result from the successive division of the two primary cells in vertical planes at right angles to the first wall; other cells are cut off from these by oblique walls, and thus an irregular spherical mass is formed.

In about thirteen days differentiation begins. Four basal cells elongate to form the primary root-cells, the position of which bears no definite relation to the direction of the supply of light (*Pl. XXI, figs. 7, 8*). Occasionally only one or two primary rhizoids are thus formed (*Pl. XXI, figs. 9, 10, 11*). Unfortunately, the plantlets died at this stage, and only by analogy could the subsequent history of the holdfasts be determined. However, the close resemblance between the primary root-cells and mature holdfasts of *Rhabdonia* and of the two species to be considered next justifies the assumption that the intermediate stages closely agree. It is interesting to note that, according to Osterhout (7), the earliest divisions in the tetraspores which give rise to proliferations do not succeed one another in the definite order just described, but the spores divide "by means of oblique walls which do not occur in regular succession."

Very similar to that of *Rhabdonia* is the early history of *Lomentaria uncinata* Menegh. and of *Champia parvula* Harv. The carpospores of *Lomentaria*, after secreting a wall, attach themselves to the substratum by a very thin mucilaginous secretion (*Pl. XXI, fig. 12*), which sometimes persists after the first rhizoids have been formed (*Pl. XXI, fig. 15*). The segmentation proceeds rapidly, but primary root-cells do not arise until a later date than in *Rhabdonia* (*Pl. XXI, figs. 13, 14*). The four basal root-cells, dividing by horizontal walls, become short, closely-appressed filaments, which soon branch pseudodichotomously (*Pl. XXI, figs. 15, 16*) and form a discoid holdfast. Strömfelt (8) regards the branching of the rhizoidal filaments as dichotomous and says that the increase in circumference of the mature holdfast is due almost entirely to marginal growth. Vegetative reproduction may take place not only by the mechanical separation of the various upright branches, which spring adventitiously from the surface of the holdfast (*Pl. XXI, fig. 22*), but by means of stolons, which are sent out in various directions and form secondary holdfasts (*Pl. XXI, fig. 21*).

Davis's account (4) of the plantlets of *Champia parvula*,

developing under natural conditions, accurately describes those grown in the laboratory. A somewhat spherical mass composed of sixteen cells results from the segmentation of the spore, then the first indication of a permanent holdfast appears as a slight projection of each of the four basal cells. The primary root-cells, dividing at right angles to their longest axis, form two-celled filaments, which branch monopodially and give rise to a broad spreading holdfast. In section the mature holdfast appears parenchymatous (*Pl. XXI, figs. 17, 18*), but it is often possible to distinguish the component filaments (*Pl. XXI, fig. 20*). Exceptional plantlets produce one instead of four primary root-cells, but the later stages conform to the type (*Pl. XXI, fig. 19*). In all cases the cells of the holdfast are paler than those of the frond, and the chromatophores of young specimens are in close contact with the walls.

From the foregoing it will be seen that *Rhabdonia*, *Lomentaria*, and *Champia* agree (*a*) in passing through a segmentation stage, resulting in a somewhat spherical mass of cells, (*b*) in the elongation of four basal cells, and (*c*) in the subsequent development of four primary rhizoids, which branch repeatedly and finally form a large discoid holdfast, composed of pseudo-parenchymatous tissue.

In marked contrast are several members of the Rhodome-laceæ. The spores of *Chondria tenuissima* (Good. et Wood.) C. Ag. and of *Chondria dasyphila* Ag. germinate very readily. The early divisions of the spores and the history of the development of the rhizoids are alike in the two species. The spores, which are large and have coarsely granular contents, quickly and firmly attach themselves to the substratum, doubtless by means of a thin and uniform layer of mucilage, though no secretion distinct from the cell-wall is perceptible (*Pl. XXI, fig. 23*). They soon divide into two unequal cells separated by a slightly concave wall; divisions parallel to the first follow (*Pl. XXI, fig. 24*), and the basal cell of the resulting filament elongates into the primary rhizoid (*Pl. XXI, figs. 25, 27*). Sometimes the basal cell seems to branch dichotomously; but, as the branches do not

arise simultaneously nor are they separated by a wall parallel to the longer axis of the basal cell, it is evident that the branching of the filaments is strictly monopodial (*Pl. XXI, figs. 26, 32, 35*). The upper cells of the plantlet soon cut off pericentral cells, and at the same period the first rhizoid divides repeatedly so as to form a multicellular, monosiphonous filament (*Pl. XXI, figs. 28, 35*). Secondary rhizoids are next developed, either as outgrowths from the primary root-cell or from a pericentral cell immediately above the basal cell (*Pl. XXI, fig. 31*). Long slender rhizoids may be formed before a clasping-disk arises, but, both in plantlets developing in the laboratory (*Pl. XXI, figs. 29, 33, 36*) and in those growing in a state of nature (*Pl. XXI, figs. 30, 38, 39, 40*), the primary rhizoid generally remains very short and by means of oblique walls produces discoid holdfasts at the tip. The size and efficiency of this holdfast are increased by means of free secondary rhizoids (*Pl. XXI, fig. 33*) or by intracuticular filaments (*Pl. XXI, fig. 34*), both of which have their origin in pericentral cells near the base of the plantlet. The secondary rhizoids develop in the same manner as the primary and combine with them to form a large, irregular, discoid holdfast, in which it is possible to distinguish few of the component filaments (*Pl. XXI, fig. 37*). The mature holdfast, though adhering closely to its host, does not penetrate it, but a cutinization of the cortical layers often results from the contact. As in Lomentaria, etc., the large holdfast gives rise to several adventitious branches; and great powers of vegetative reproduction are implied by the stores of floridean starch with which the cells are often charged. The chromatophores are closely aggregated in the peripheral protoplasm, especially next to the inner radial and the lateral walls, and often indicate the plane in which a wall will soon be formed. They are large and discoid, thus resembling those of the cortical cells of the frond rather than the anastomosing filamentous chromatophores of the central cells.

Very different from the short, multicellular, primary rhizoids of the Chondriæ are the primary holdfasts of the Polysiphoniæ. The form taken as a type of the latter group is

Polysiphonia violacea (Roth) Grev. In a few hours after they are sown, both carpospores and tetraspores attach themselves to the substratum by a coarsely granular, mucilaginous secretion, which completely covers the spore (*Pl. XXI, fig. 41*). In optical section this envelope appears densely granular at the margin, while a clear amorphous area intervenes between the outer layer and the developing plantlet (*Pl. XXI, fig. 44*). The spore divides into two unequal cells, of which the smaller soon becomes slightly pointed, and finally grows into the primary root-cell (*Pl. XXI, fig. 42*). Divisions parallel to the first ensue (*Pl. XXI, figs. 43-45*), and the basal-cell elongates so as to form the first rhizoid piercing the mucilaginous sheath, which finally disintegrates and disappears. A six-celled stage is often reached before divisions in planes at an angle to the first occur. Generally, segmentation continues for some time and the siphons are clearly marked off from the central axis before a second rhizoid arises. As in *Chondria*, this has its origin in an unsegmented cell adjacent to the primary root-cell. The former differs from the latter only in its brighter color and denser cell-contents; and, remaining undivided, it forms a component part of the holdfast (*Pl. XXII, fig. 3*). The protoplasmic connections between these cells are obvious, but they are difficult to trace between the other cells of the plantlet (*Pl. XXI, figs. 45, 47*). When three or four weeks old the young plant develops several rhizoids springing either from the primary or secondary root-cell (*Pl. XXII, fig. 7*). Occasionally, however, the segmentation stage of the spore ends and the growth of the frond begins before multiplication of the rhizoids takes place (*Pl. XXII, fig. 10*). At the base of the frond other rhizoids are sent out by corticating cells and are separated from these by a wall, a protoplasmic connection being maintained. No intracuticular filaments are developed and the independence of the rhizoidal constituents of the mature holdfast is practically preserved (*Pl. XXII, fig. 6*). In addition to the rhizoids near the base of the plant, any corticating cell of a procumbent branch may produce a secondary holdfast and thus assist in the extension of the colony. As Strömfelt (8) noted,

all the rhizoids are unicellular and unbranched; and, although an apparent tendency to branch may be observed occasionally, the lobes are not separated from the main portion by a wall, even the protoplasmic contents being undivided (*Pl. XXII, fig. 9*). All the rhizoids eventually develop terminal clasping-disks. The first indication of such a structure may appear in plantlets four days old, but, as a rule, the primary rhizoids do not undergo modification until several days later. The disks begin as a simple enlargement of the tip of the rhizoid (*Pl. XXI, figs. 48-50; XXII, fig. 1*), become deeply lobed, and assume a very irregular outline (*Pl. XXI, figs. 52-56*). The cell-contents of the rhizoid extend into the lobes, but no division takes place (*Pl. XXII, fig. 8*). Great variations in the length attained by the primary rhizoids occur both in plants grown under natural conditions and in laboratory cultures (*Pl. XXI, figs. 46, 48; XXII, fig. 1*). The cause of such variations has not been determined, but it is probable that contact irritation may be the most important factor in the formation of the disks. This view is supported by the fact that disks are sometimes produced on the sides of rhizoids when these come in contact with a firm substance (*Pl. XXII, figs. 4, 5*). The length of the secondary rhizoids depends upon the distance of the parent cells from the substratum, and as soon as contact is established broad clasping-disks are formed, which mechanically cohering with one another and with the primary disk produce a very strong holdfast. The rhizoids are paler in color than the rest of the plantlet, having less dense contents and fewer chromatophores.

The rhizoids of *Polysiphonia violacea* never penetrate the host-plant; but at the point of contact the surface of the latter is often dark brown and cutinized, while the outer cortical cells are destitute of chromatophores. But incipient parasitism occurs in *Polysiphonia fastigiata* Grev., growing on *Ascophyllum nodosum* Stack. Gibson (5), in writing of the histology of this species, noticed that "the attachment of the epiphyte to *Ascophyllum* is very intimate. Root-filaments given off from the base of the frond penetrate deeply into the tissue of the host, and wander

among the cortical cells and medullary hyphæ. The root-filaments have very thick cell-walls and central cells only, these being much elongated." The ends of the rhizoids are swollen and in close contact with the cells of the host (*text figs. 4, 5, p. 256*), but no haustoria penetrate the walls of the latter. In one instance a unique variation occurred. A few intracuticular filaments, descending from the corticating cells of the *Polysiphonia*, ran parallel to the main axis of the rhizoid throughout its length. The host suffers no serious injury, only a depression and cutinization of the surface with a very slight disorganization of the cortical cells at the point of penetration. Though the association of the two plants does not justify the assumption of complete parasitism, the symbiotic relation existing between them is much more intimate than that observed between *Ascophyllum* and any of the truly epiphytic algæ. According to Brebner (3), a similar relation exists between *Dumontia filiformis* and its host, *Fucus serratus*.

Dasya elegans (Martens) C. Ag. was the third species of the Rhodomelaceæ examined. The spores attach themselves by a mucilaginous secretion much less definite in form and less persistent than in *Polysiphonia violacea* (*Pl. XXII, fig. 30*). The spore elongates before the division takes place, and in many instances the very young plantlet assumes an hour-glass shape, occasionally with a delicate mucilaginous secretion at either end. The first walls are parallel to one another, forming a long filamentous body, of which one terminal cell becomes the apical cell of the frond, the other the primary root-cell (*Pl. XXII, figs. 31, 32, 33, 35, 36*). Twelve or more parallel divisions may occur before the basal cell elongates and forms a rhizoid terminating in a disk; but such a modification may appear at an earlier period (*Pl. XXII, fig. 34*). The multicellular disks, which arise sooner or later, are like those of *Chondria*. The root-cell or the end of a rhizoid broadens and becomes slightly lobed; oblique walls cut off the lower corners of the cell; division is continued and a multicellular disk with a mucilaginous margin results (*Pl. XXII, figs. 39-41; XXIII, figs. 2, 3, 7, 8, 9*). The primary root

cell often branches, each portion giving rise to a disk (*Pl. XXII, fig. 42; XXIII, fig. 4*). Although the primary rhizoid usually remains short, in some instances it attains considerable length before undergoing division or forming a disk (*Pl. XXII, figs. 37, 38*). While these changes are taking place, the cell adjacent to the basal cell sends out rhizoids similar to those arising from the primary root-cell (*Pl. XXIII, figs. 1, 5, 6*). These various root-filaments combine to form the primary holdfast, which is afterwards strengthened by multicellular branching rhizoids, springing from the basal corticating cells of the frond. The course of the filaments may be traced for some distance in the holdfast, but it is difficult to distinguish between those cells which have their origin in the primary disk and those which are derived from the corticating filaments. The difficulty in determining the relationship of the parts is increased by secondary lateral connections, which are developed between the corticating cells (*Pl. XXII, fig. 43*). The marginal cells of the mature holdfast are larger and broader in proportion to their length than the corticating cells of the fronds, and have denser cell-contents, but the chromatophores of both are separate disks, while those of the central siphon are the anastomosing filaments characteristic of many of the Rhodomelaceæ. A creeping tendency may be exhibited at an early age, very young plantlets sometimes developing two distinct holdfasts of almost equal importance (*Pl. XXIII, fig. 4*). As in the other species described, many branches arise from the massive rounded holdfast, probably springing adventitiously from the surface of the latter.

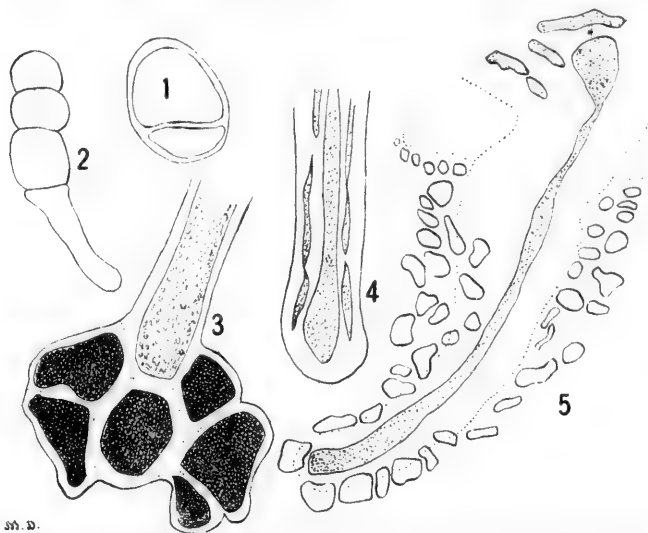
A comparison of the three species of the Rhodomelaceæ described will show that they agree in forming a primary root-cell, which elongates into a rhizoid terminating in a clasping disk; and in developing secondary rhizoids, which are sent out by the root-cell, the cell adjacent to it, and the cortical cells at the base of the frond. But, while the rhizoids of Polysiphonia are unicellular, unbranched, and free, those of *Dasya* and *Chondria* are multicellular, branched, and aggregated into a compact cell-mass, which in section resembles parenchymatous tissue.

The species remaining for consideration belong to the Ceramiales. Cultures of *Spermothamnion Turneri* Aresch. were unsuccessful, only one healthy plantlet having been obtained. It developed two small disks, the one a terminal primary holdfast, the other a secondary structure arising from one of the middle cells of the filament (*Pl. XXIII, fig. 41*). As Strömfelt has pointed out, the mature rhizoids are short, unicellular, unbranched organs, terminating in a lobed disk in which delicate threads of protoplasm can be traced (*Pl. XXIII, figs. 42, 43*). The rhizoids are especially abundant near the base of the plants, but, as is well known, any cell of a procumbent branch may give rise to these simple bodies. Now and then, an ordinary branch of the frond produces at its apex a much-lobed twisted disk, which closely embraces a neighboring branch as a tendril would a support (*Pl. XXIII, fig. 40*).

Very few spores of *Griffithsia Bornetiana* Farlow germinated, and the resulting plantlets were short-lived. It is, therefore, impossible to describe each step in the development of the holdfast. Two unequal cells arise from the first division (*text fig. 1*), a monosiphonous filament composed of rather globose cells is formed, the basal cell of which elongates and becomes the root-cell (*text fig. 2*). The structure of mature holdfasts would lead one to suppose that the primary root-cell divides repeatedly, forming a broad spreading mass of large-celled pseudo-parenchymatous tissue. The holdfasts of a young plant attached to a small piece of bone (*text fig. 3*) and of older plants growing on *Zostera marina* L. differed only in size, that of the latter being very large with an abundance of adventitious branches arising from its margin. Strömfelt (8) places the genus *Griffithsia* with *Ceramium* and *Callithamnion* in a group distinguished by branching rhizoids; but, though many mature specimens of *Griffithsia Bornetiana* were examined, no such secondary formations were seen. The cells of the holdfasts are brilliantly colored and have very dense granular contents, probably due to a large supply of reserve food-material.

A closely allied genus, *Callithamnion*, differs greatly from

Griffithsia in the form and history of the holdfast. Though the spores of *Callithamnion Borreri* Ag. developed in the laboratory with difficulty, cultures sufficient to illustrate the order of development succeeded. After attaching themselves to the slide by an almost imperceptible secretion, the spores elongate and become pointed at both ends. The first division is parallel to the shorter axis (*Pl. XXIII, fig. 29*), and by subsequent partition a



C. S. D.

FIG. 1. *Griffithsia Bornetiana* Farlow, germinating tetraspore 9 days after sowing. $\times 333$.

FIG. 2. *G. Bornetiana*, plantlet 9 days old. $\times 213$.

FIG. 3. *G. Bornetiana*, holdfast of small plant growing on bone. $\times 53$.

FIGS. 4, 5. *Polysiphonia fastigiata* Gréville, growing on *Ascophyllum nodosum* Stack.; in fig. 5 the cells of *P. fastigiata* are shaded in, those of *Ascophyllum* are merely outlined. $\times 213$.

monosiphonous filament is formed. The smaller of the two terminal cells is the primary root-cell (*Pl. XXIII, fig. 30*). Judging from one set of cultures, the first cell of the holdfast, which has a very thick mucilaginous wall, is cut off from the swollen

extremity of the root-cell and separated from it by a wall (*Pl. XXIII, figs. 31-33, 37, 38*). A multicellular holdfast results from the division and branching of the primary root-cell and of the oldest cell of the disk (*Pl. XXIII, figs. 34, 36*), and is further strengthened by a few corticating rhizoidal filaments. In mature *Callithamnion Baileyi* Harv. the intracuticular rhizoids are more numerous. They arise from the lower angles of the central cells or from the basal cells of the branches. Thence they descend through the walls of the monosiphonous frond to the holdfast, where they branch freely and spread out in various directions, forming, with the filaments arising from the cells of the primary disk, a flat circular holdfast (*Pl. XXIII, figs. 35, 39*).

The carpospores of *Spyridia filamentosa* (Wulf.) Harv. germinate very readily. The mucilaginous secretion, by which the spores are first fastened to the substratum, can hardly be distinguished from the wall of the spore (*Pl. XXII, fig. 11*). The spore first forms two unequal cells, the smaller of which becomes the primary root-cell, the larger divides by parallel walls so as to form a short filament (*Pl. XXII, figs. 12-14*). As a rule, no long primary rhizoid is formed, but occasional exceptions are found (*Pl. XXII, fig. 18*). Though variations may occur (*Pl. XXII, fig. 15*), the first corticating cells are usually cut off from the upper angles of the central cells before the formation of the discoidal holdfast begins (*Pl. XXII, fig. 16*). Sooner or later, however, the primary root-cell divides in several planes parallel to the longer axis of the spore, and thus produces a flat multicellular disk, the cells of which are separated by walls (*Pl. XXII, figs. 15, 17, 19, 20, 21*). At first the primary disk is but slightly lobed, but the cells soon give rise to short filamentous outgrowths, which branch pseudo-dichotomously (*Pl. XXII, figs. 21, 22*). Rarely a lateral disk springs from the primary root-cell, which is then prolonged into a filament (*Pl. XXII, fig. 23*). The cells of the primary holdfast continue to divide, and with them are combined rhizoidal filaments, which have their origin in the corticating cells of the lower nodes of the frond and grow through the cell-walls to the substratum (*Pl. XXII, figs. 24, 25*). Free filamentous

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outgrowths of the larger cortical cells develop disks and enter into close mechanical union with the main holdfast, adding greatly to its efficiency. The secondary rhizoids thus formed are destitute of cortications (*Pl. XXII, fig. 29*) and are easily distinguished from those ordinary branches which, coming in contact with the substratum, develop holdfasts (*Pl. XXII, figs. 26, 28 a*). *Spyridia* creeps not only by means of such branches but by the aid of masses of uncorticated hair-like rhizoids, which may be formed at any point (*Pl. XXII, fig. 28 b*). One curious instance was noted of short rhizoidal outgrowths from each of the central cells of a trailing branch, the cortical cells being unmodified (*Pl. XXII, fig. 27*). The differences in the chromatophores are similar to those noted in the Rhodomelaceæ.

Ceramium differs in many respects from the other genera described. Both *Ceramium rubrum* (Huds.) C. Ag. and *C. strictum* Harv. were carefully studied and found to agree closely in so far as the early development of the plantlet and the formation of the rhizoid are concerned. Shortly after it is sown, the spore produces a cell-wall (*Pl. XXIII, fig. 24*) and a well-defined temporary holdfast. The latter is a granular disk of definite thickness, and mucilaginous in character, attached to the base of the spore (*Pl. XXIII, fig. 10*). The granules, embedded in a clear matrix, are often arranged in lines radiating from the axis to the rim of the disk (*Pl. XXIII, fig. 25*). The distances between the granules being least in vertical planes, the disk appears densest when viewed from the side. This peculiar body does not respond to the ordinary test for cellulose, and is not dissolved after prolonged treatment with dilute potassium hydrate. It is affected neither by Hanstein's aniline blue nor safranin; but the granular portions stain deeply with hæmatoxylin and with Congo-red and the whole with Bismarck-brown. The disk is, therefore, distinct from the cellulose wall of the spore, and differs materially from ordinary vegetable mucilages, though it is probably closely allied to the latter. This temporary holdfast is not peculiar to plants existing in an unnatural environment, but has been found in very young plants growing on *Chordaria*. As the

spore develops, the first rhizoid pierces the disk, which then becomes disintegrated and finally disappears (*Pl. XXIII, fig. 26*).

After attaching itself in the manner described, the spore elongates and divides several times in parallel planes at right angles to its longer axis (*Pl. XXIII, figs. 11-13*). The basal cell, growing rapidly, produces a multicellular rhizoid at an early age; but large plantlets, which have already cut off corticating cells, occasionally show little or no tendency to form rhizoids (*Pl. XXIII, figs. 14, 15, 18*). The primary root-cell branches into several rhizoids, which are increased in number by outgrowths from the cell adjoining the first root-cell (*Pl. XXIII, figs. 17, 19, 20, 27*). Still later, the cortications near the base of the plantlet develop multicellular branching rhizoids of great length. All remain free throughout the life of the plant, and both primary and secondary rhizoids branch monopodially near the tip, and thus give rise to large multicellular disks of irregular outline (*Pl. XXIII, figs. 13, 22, 26, 28*). These indented clasping-disks are closely crowded together, cohering so as to form a large rounded holdfast, in which the various elements may be clearly distinguished. As both of the species are upright in habit, no secondary holdfasts are developed at any point of the mature frond. As in several other genera, the chromatophores of the plantlets and of the holdfasts resemble those of the corticating cells rather than those of the central axis, the former being disks, the latter irregular branching bands (*Pl. XXIII, figs. 17 and 21*).

It is evident, therefore, that the species of the Ceramiaceæ examined differ greatly both in the manner of development and the form of the holdfast, agreeing only in the production of one primary root-cell. *Spermothamnion Turneri* forms at various points short unicellular rhizoids with terminal disks, branching does not occur, and cortications are not developed. *Griffithsia Bornetiana* produces a large spreading holdfast composed entirely of a pseudo-parenchymatous tissue arising from the primary root-cell. *Callithamnion*, *Spyridia*, and *Ceramium* have primary

root-cells, from which spring rhizoids terminating in multicellular disks. Others originate in the cell adjacent to the basal cell and in the cortications. In addition the first two possess a strengthening mass of intracuticular root-fibers, but *Ceramium* is quite destitute of them.

Thus, while of some value in showing relationships, it will be seen that the chief interest in a comparative study of the developing spores and holdfasts of the Florideæ would be in variations dependent upon differences in light, temperature, or the density of the surrounding medium, and in adaptations to vegetative reproduction.

In closing, I would acknowledge my indebtedness to Dr. Setchell, who, in 1895, suggested the holdfasts of the Rhodophyceæ as a subject that would repay investigation; to the late Dr. Humphrey, under whose helpful and suggestive direction the work described in this paper was practically begun; and to Professor Penhallow for kind advice.

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EXPLANATION OF PLATES XXI-XXIII.

PLATE XXI.

- FIG. 1. *Rhabdonia tenera* J. Ag., carpospore 9 hrs. after sowing. $\times 334$.
FIG. 2. *R. tenera*, 2 days old. $\times 334$.
FIGS. 3-11. *R. tenera*, from 4 to 17 days old. $\times 334$.
FIG. 12. *Lomentaria uncinata* Menegh., carpospore. $\times 334$.
FIGS. 13-15. *L. uncinata*, 6 days old. $\times 334$.
FIG. 16. *L. uncinata*, an unusually large specimen, 6 days old. $\times 213$.
FIGS. 17-19. *Champia parvula* Harv., plantlets resulting from the germination of carpospores, 8 days old. $\times 334$.
FIG. 20. *C. parvula*, holdfast of a plantlet growing on *Polysiphonia*. $\times 213$.
FIGS. 21, 22. *Lomentaria uncinata*, bases of mature plants.
FIG. 23. *Chondria tenuissima* (Good. et Wood) C. Ag., tetraspore shortly after it was sown. $\times 233$.
FIGS. 24-28. *C. tenuissima*, plantlets developed from carpospores, from 2 to 4 days old. $\times 233$.
FIG. 29. *C. tenuissima*, plantlet resulting from the germination of a tetraspore, 10 days old. $\times 233$.
FIG. 30. *C. tenuissima* found growing on mature *Chondria*. $\times 233$.
FIGS. 31, 32. *C. tenuissima*, 3 days old. $\times 233$.
FIG. 33. *C. tenuissima*, 12 days old. $\times 213$.
FIG. 34. *C. tenuissima*, 14 days old. $\times 213$.
FIGS. 35, 36. *C. tenuissima*, 5 days old. $\times 213$.
FIG. 37. *C. tenuissima*, portion of mature holdfast, stained with methyl blue. $\times 213$.
FIGS. 38-40. *C. tenuissima*, holdfasts of plants found growing on mature *Chondria*, stained with methyl blue. $\times 333$.
FIGS. 41-56. *Polysiphonia violacea* (Roth) Greville.
FIGS. 41-45. Carpospore and plantlets from 1 to 5 days old. $\times 400$.
FIG. 46. Plantlet 7 days old. $\times 633$.
FIGS. 47, 48. Plantlets found growing on *Scytosiphon lomentarius* Ag. $\times 400$.
FIG. 49. Plantlet, result of germinating carpospore. $\times 213$.
FIGS. 50-56. Ends of primary rhizoids of plantlets 12 days old. $\times 400$.

PLATE XXII.

FIGS. 1-10. *Polysiphonia violacea* (Roth) Grev.FIG. 1. Plantlet growing on *Scytosiphonolomentarius* Ag. $\times 400$.FIG. 2. Plantlet 3 days old. $\times 400$.FIG. 3. Plantlet 9 days old. $\times 400$.FIGS. 4, 5. Plantlets 12 days old. $\times 233$.FIG. 6. Holdfast showing rhizoids springing from corticating cells. $\times 54$.FIG. 7. Plantlet 12 days old. $\times 213$.FIG. 8. Clasp disk of rhizoid of plant growing on *Zostera marina* L. $\times 400$.FIGS. 9, 10. Plantlets 9 and 11 days old. $\times 400$.FIGS. 11-29. *Spyridia filamentosa* (Wulf.) Harv.FIG. 11. Carpospore. $\times 400$.FIGS. 12-18. Plantlets from 2 to 12 days old. $\times 400$.FIGS. 19-23. Bases of plantlets, showing primary cells and clasping disks. $\times 400$.FIG. 24. Base of rhizoidal branch (c. of fig. 28). $\times 213$.FIG. 25. Edge of mature holdfast, in optical section. $\times 157$.

FIG. 26. Transverse section of frond, showing that the origin of rhizoidal branches is in the corticating cells; somewhat magnified.

FIG. 27. Procumbent branch, near 18a, with rhizoidal outgrowths from central cell. $\times 333$.

FIG. 28. Creeping branch, slightly magnified.

FIG. 29. Uncorticated secondary rhizoid with disk. $\times 333$.FIGS. 30-43. *Dasya elegans* (Martens) C. Ag.FIGS. 30, 31. Germinating tetraspore. $\times 400$.FIG. 32. Segmenting carpospore 2 days old. $\times 400$.FIGS. 33-35. Segmenting tetraspore. $\times 400$.FIGS. 36-38. Plantlets 12 days old, resulting from the germination of tetraspores. $\times 400$.FIGS. 39-42. Plantlets 17 days old, resulting from the germination of carpospores; figs. 39, 42 show only the root-cell and disk. $\times 400$.FIG. 43. Portion of mature holdfast, in optical section. $\times 233$.

PLATE XXIII.

FIGS. 1-9. *Dasya elegans* (Martens) C. Ag. Plantlets resulting from the germination of carpospores; in some cases only the primary root-cell and disk are shown; from 12 to 20 days old. $\times 400$.

FIGS. 10-23. *Ceramium rubrum* (Huds.) C. Ag.

FIG. 10. Germinating carpospore 2 days after sowing. $\times 633$.

FIGS. 11-17. Plantlets from 3 to 8 days old; in *figs. 15, 16* only the basal cells and primary rhizoids are shown. $\times 400$.

FIG. 18. Plantlet found growing on Polysiphonia. $\times 400$.

FIGS. 19, 20. Plantlets 9 days old. $\times 400$.

FIG. 21. Plantlet growing on Polysiphonia. $\times 400$.

FIG. 22. Plantlet 5 days old, showing early branching of the primary rhizoid. $\times 400$.

FIG. 23. Holdfast of a rather young plant. $\times 213$.

FIGS. 24-28. *Ceramium strictum* (Harv.).

FIG. 24. Carpospore 36 hours after it was sown. $\times 400$.

FIG. 25. Plantlet 3 days old. $\times 233$.

FIGS. 26, 27. Plantlets about 7 days old. $\times 400$.

FIG. 28. Primary root-cell and disk of mature plant. $\times 400$.

FIGS. 29-32. *Callithamnion Borreri* Ag., plantlets from 2 to 6 days old. $\times 213$.

FIG. 33. *C. Borreri*, plantlet showing basal cell and rudimentary disk, 6 days old. $\times 213$.

FIG. 34. *C. Borreri*, primary disk of plantlet 9 days old. $\times 333$.

FIG. 35. *C. Baileyi* Harv., mature holdfast, in optical section. $\times 213$.

FIGS. 36, 37. *C. Borreri*, base of plantlets 6 days old, each showing primary disk. $\times 400$.

FIG. 38. *C. Borreri*, plantlet 6 days old. $\times 213$.

FIG. 39. *C. Baileyi*, a portion of a mature holdfast. $\times 100$.

FIG. 40. *Spermothamnion Turneri* Aresch., branch with clasping disk. $\times 213$.

FIG. 41. *S. Turneri*, plantlet 6 days old; nine cells of the filament are not represented. $\times 213$.

FIGS. 42, 43. *S. Turneri*, mature holdfast. $\times 213$.

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